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# NOTES ON THE LESSER ONE-HORNED RHINOCEROS, *RHINOCEROS SONDAICUS*

## 2. THE POSITION OF *RHINOCEROS SONDAICUS* IN THE PHYLOGENY OF THE GENUS *RHINOCEROS*

BY EDWIN H. COLBERT

Although there is a fairly extensive literature on the so-called Javan rhinoceros, *Rhinoceros sondaicus*, this form has been generally neglected in discussions having to do with the phylogenetic development of the Rhinocerotidae. It is true, of course, that various authors have recognized *Rhinoceros sondaicus* as an animal less "specialized" or less "modified" than the Indian rhinoceros, *Rhinoceros unicornis* (Osborn, 1898; Matthew, 1931), but beyond such general statements as to its phylogenetic relationships there has been little or no effort made to discuss in a detailed way the affinities of this extraordinarily rare and interesting mammal. Perhaps this neglect of *Rhinoceros sondaicus* in the more general discussions of phylogeny within the family Rhinocerotidae has been due, to a considerable extent, to the comparative rarity of the species in museums, or at least to the lack of acquaintance with this animal by palaeontologists. For it is only through a palaeontological background, particularly a knowledge of the late Tertiary and Quaternary rhinoceroses of Asia, that the true position of *Rhinoceros sondaicus* in its relationships to other rhinoceroses can be completely appreciated.

It was the good fortune of the present author to be engaged in a study of the extinct rhinoceroses from the Pleistocene of China—as part of a general study of the Pleistocene mammalian fauna from the limestone fissures of Szechwan—when the skull of *Rhinoceros sondaicus* in the American Museum came to light. When this recent skull was examined, certain implications as to its relationships to some of the Asiatic Pleistocene forms became at once apparent, thereby affording a much clearer picture of the phylogenetic development of the genus *Rhinoceros* than had previously been envisioned by the writer. Consequently it has been thought advantageous to discuss briefly the evolution of *Rhinoceros* (using the term in a strict sense) in an effort to show how *Rhinoceros sondaicus* may be related to other species of the genus.

In the first place, it might be well to indicate the limits of the genus *Rhinoceros*. This genus has been used, particularly by palaeontologists, to include a great number of species ranging in age from the Miocene through the Pleistocene and into Recent times. Indeed, during the early history of vertebrate paleontology it was the practice to designate almost every fossil rhinoceros of post-Oligocene age as *Rhinoceros*, since in those days students of fossils naturally were but little concerned with the critical limitations for genera and species that have developed with the refinement of the science.

Obviously this is wrong and has been so recognized with the increasingly detailed studies that have been made in later years on fossil vertebrates. Consequently at the present time most of the fossil species formerly designated as *Rhinoceros* have been allocated to other genera, and the genus has thus become strictly limited according to the evidence of its anatomical characters, which, as far as the osteology of the skull and the dentition are concerned, are as follows:

1. Expansion of the nasal bones into a boss or eminence, upon which is borne the single nasal horn.
2. Incisors present, and of large size.
3. Skull short, with occipital plane inclined forward.
4. Auditory meatus closed inferiorly by fusion of the post-tympanic and the post-glenoid processes.
5. Cheek teeth sub-hypsodont.

Upon the basis of the above limitations, the genus *Rhinoceros* includes four good species, two of which are of recent age, and two of which are extinct. There are other fossil species of doubtful validity which need not be considered at this place. The four species with which we are concerned are:

*Rhinoceros unicornis* Linnaeus, 1758. Type of genus.

Synonyms: *R. indicus, R. asiaticus, R. stenocephalus.*

Pleistocene and Recent of India. Now very limited in range.

*Rhinoceros sondaicus* Desmarest, 1822.

Synonyms: *R. javanicus, R. inermis, R. nasalis, R. floweri.*

Possibly Pleistocene (of Borneo) and Recent of the Sundarbans, eastern Bengal, Assam, Burma, Malay Peninsula, Sumatra and Java.

*Rhinoceros sivalensis* Falconer and Cautley, 1847.

Synonym: *R. palaeindicus.*

Pleistocene of the Siwalik Hills of India.

*Rhinoceros sinensis* Owen, 1870.

Synonyms: *R. plicidens, R. simplicidens.*

Pleistocene of southwestern China.

It might be well at this place to indicate the distinctions in the skull, jaw and dentition between the two recent species, *Rhinoceros unicornis* and *Rhinoceros sondaicus*, since many of these distinctions are of considerable importance in the following discussion of the phylogenetic position of each species in relation to the other. Moreover, by calling attention to these osteological differences between the two modern species it may be that some aid will be afforded to workers in the future who may have occasion to examine skulls and teeth of *Rhinoceros*.

Flower (1876) published a paper in which he described many of the distinguishing traits between the two living species of *Rhinoceros*, while Osborn in his monograph

SKULL, MANDIBLE AND DENTITION

| *Rhinoceros unicornis* | *Rhinoceros sondaicus* |
|---|---|
| 1. Large and robust. | 1. Smaller and lighter than *R. unicornis*. |
| 2. Nasals expanded into large, rounded horn boss. | 2. Less expansion in the nasals; horn boss pointed rather than rounded, and very small in female. |
| 3. Ascending ramus very high. | 3. Ascending ramus not extremely heightened. |
| 4. Occipital surface high and narrow. Skull deep. | 4. Occipital surface comparatively low and broad. Skull comparatively shallow. |
| 5. Deep "saddle" in profile of skull, between nasals and occipital vertex. | 5. Rather shallow saddle in cranial profile. |
| 6. Zygomatic arch rounded at posterior termination. | 6. Zygomatic arch angular at posterior termination. |
| 7. Posterior margin of palate concave, or with small median projection. | 7. Posterior margin of palate with median projection. |
| 8. Mesopterygoid fossa, basisphenoid and basioccipital bones narrow. | 8. Mesopterygoid fossa, basisphenoid and basioccipital bones comparatively broad. |
| 9. Pterygoids compressed and grooved. | 9. Pterygoids flattened and laterally expanded. |
| 10. Vomer thick and united to sides of pterygoid processes. | 10. Vomer thin, lamelliform, pointed and free. |
| 11. Premaxillaries broad. | 11. Premaxillaries relatively narrow. |
| 12. Teeth strongly sub-hypsodont. | 12. Teeth less hypsodont than in *R. unicornis*. |
| 13. Ectoloph of cheek teeth rather flat. | 13. Ectoloph of cheek teeth sinuous. |
| 14. Parastyle buttress suppressed. | 14. Parastyle buttress prominent. |
| 15. Well-developed crochet and crista, united in worn tooth to enclose a medifossette. | 15. Crochet present but crista generally absent. |

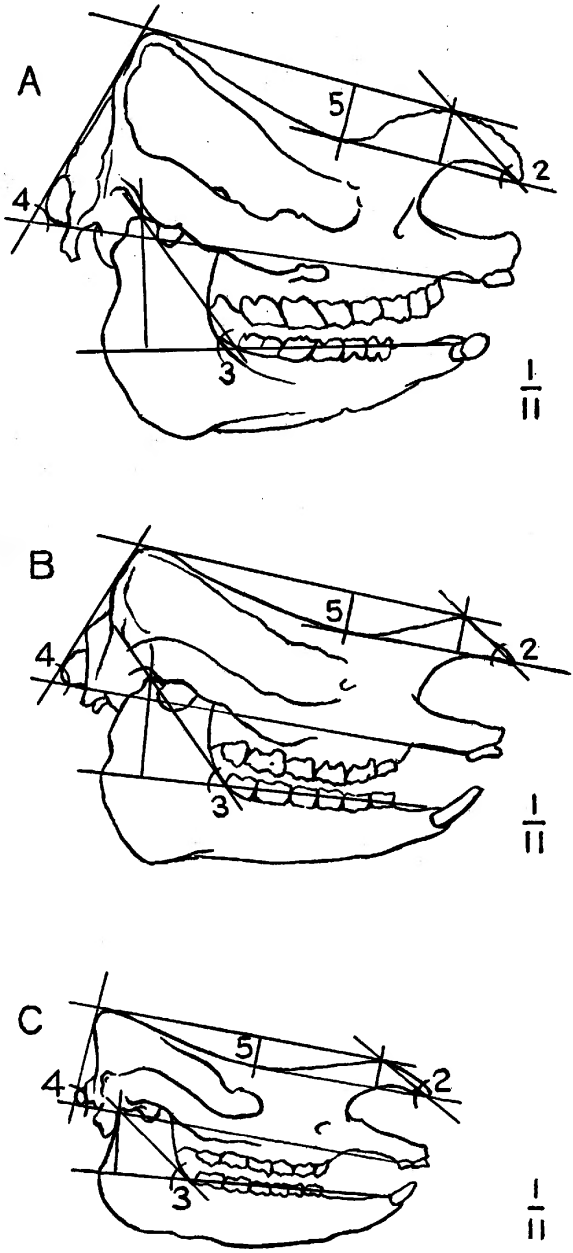


Fig. 1. Comparison of the skull and jaw of (A) *Rhinoceros unicornis*, (B) *Rhinoceros sondaicus* and (C) *Gaindatherium browni*. Lateral views of right side showing, from C to B to A: (2) increase of nasal horn boss, (3) increase in height of ascending ramus, (4) increase in height and forward inclination of occiput, (5) increase in depth of "saddle" in cranial profile.

Compare the items with these same numbers on page 2.

Figures one-eleventh natural size A and B from Osborn, 1898; C from Colbert 1934.

on "The Extinct Rhinoceroses" (1898) discussed briefly certain differences to be seen between the living species of *Rhinoceros*, and in addition presented a very useful comparative figure in which lateral views of the skulls and mandibles of all the living rhinoceroses were shown to scale. Upon the basis of these previously published works and original observations of the American Museum specimens of *Rhinoceros*, the accompanying comparison has been drawn up (see p. 2).

This comparison of the characters in the two modern species of *Rhinoceros* is interesting in that it shows what might be called a "harmonic" specialization of *Rhinoceros*

*unicornis* over *Rhinoceros sondaicus*. The one species is advanced beyond the other not by virtue of a few isolated characters but in all features throughout the structure of the skull, jaws and dentition; every character listed above for the distinction of the two forms shows an advance in the Indian rhinoceros over its expression in the Javan form. It is not possible on the basis of the material available to compare skeletons of the two species, but it would seem likely that much the same picture would hold in a lesser degree in the post-cranial region. Certainly the external characters in the two species conform to this conception of a general, all-round specialization of *Rhinoceros unicornis* over *Rhinoceros sondaicus*.

The validity and the direction of the specializations in *Rhinoceros*, shown in two successive stages by the modern species, are corroborated by a study of the fossil material, particularly the evidence offered by the extinct genus *Gaindatherium* from the late Tertiary phases of the Siwalik series of India, described a few years ago by the present author (Colbert, 1934). When it was described, *Gaindatherium* was suggested as an ancestor to *Rhinoceros*, the comparison being between the fossil form and the Indian animal. With a skull of *Rhinoceros sondaicus* at hand it can now be seen how nicely the Javan rhinoceros fits as a form intermediate in position between *Gaindatherium* and *Rhinoceros unicornis*.

Every character that sets *Rhinoceros sondaicus* off from *Rhinoceros unicornis* is expressed with greater emphasis in *Gaindatherium*. This is conveniently shown when *Gaindatherium* is compared point by point with *Rhinoceros sondaicus*, using the numbers that were listed in the comparison, presented above, of the two living species.

*Gaindatherium browni* COMPARED WITH *Rhinoceros sondaicus*

1. *Gaindatherium* is smaller and lighter than *Rhinoceros sondaicus*.
2. Less expansion of the nasals; horn boss pointed.
3. Ascending ramus lower.
4. Skull generally lower. (The occiput of *Gaindatherium* is vertical, a primitive character as compared with the forwardly inclined occiput of *Rhinoceros*.)
5. Shallower saddle in cranial profile.
6. Zygomatic arch more angular at posterior termination.
7. Posterior margin of palate with small median projection.
11. Premaxillaries narrow. (Two incisor teeth, a primitive character.)
12. Teeth more brachyodont than in *R. sondaicus*.
13. Ectoloph of cheek teeth sinuous.
14. Parastyle buttress prominent.
15. Neither crista nor crochet present.

It might be mentioned that in these characters *Gaindatherium* in turn is more or less intermediate between *Rhinoceros sondaicus* and certain mid-Tertiary rhinoceroses such as *Caenopus* or *Subhyracodon*. The reason that *Gaindatherium* is thought to be directly ancestral to *Rhinoceros* is its possession of certain characters mentioned in an earlier paragraph that distinguish the latter genus, specifically the presence of a single nasal horn and the consequent development of a saddle-shaped cranial profile, the presence of large, well-developed incisors and the closure of the external auditory meatus inferiorly by the fusion of the post-tympanic and post-glenoid processes.

At this place it might be well to consider briefly two Pleistocene species of *Rhinoceros*, *Rhinoceros sinensis* and *Rhinoceros sivalensis*, both known from considerable suites of materials from China and India, respectively.

*Rhinoceros sinensis* is a large species, almost as big as the modern Indian rhinoceros, but interesting in that it shows a combination of the characters that distinguish *R. sondaicus* and *R. unicornis*. Thus, in spite of its large size, *Rhinoceros sinensis* seemingly had a rather small horn carried on a pointed horn boss, as in the Javan rhinoceros. Since the back of the skull is not well preserved in this species, nothing can be said about the diagnostic characters of the cranial and basicranial regions. However, the cheek teeth are interesting in that they are hypsodont, more so than the teeth of *Rhinoceros sondaicus*, less so than those of *Rhinoceros unicornis*, they have the parastyle buttress as in *R. sondaicus* but not so prominent, the ectoloph is less sinuous than in *R. sondaicus* but not so flattened as in *R. unicornis*,

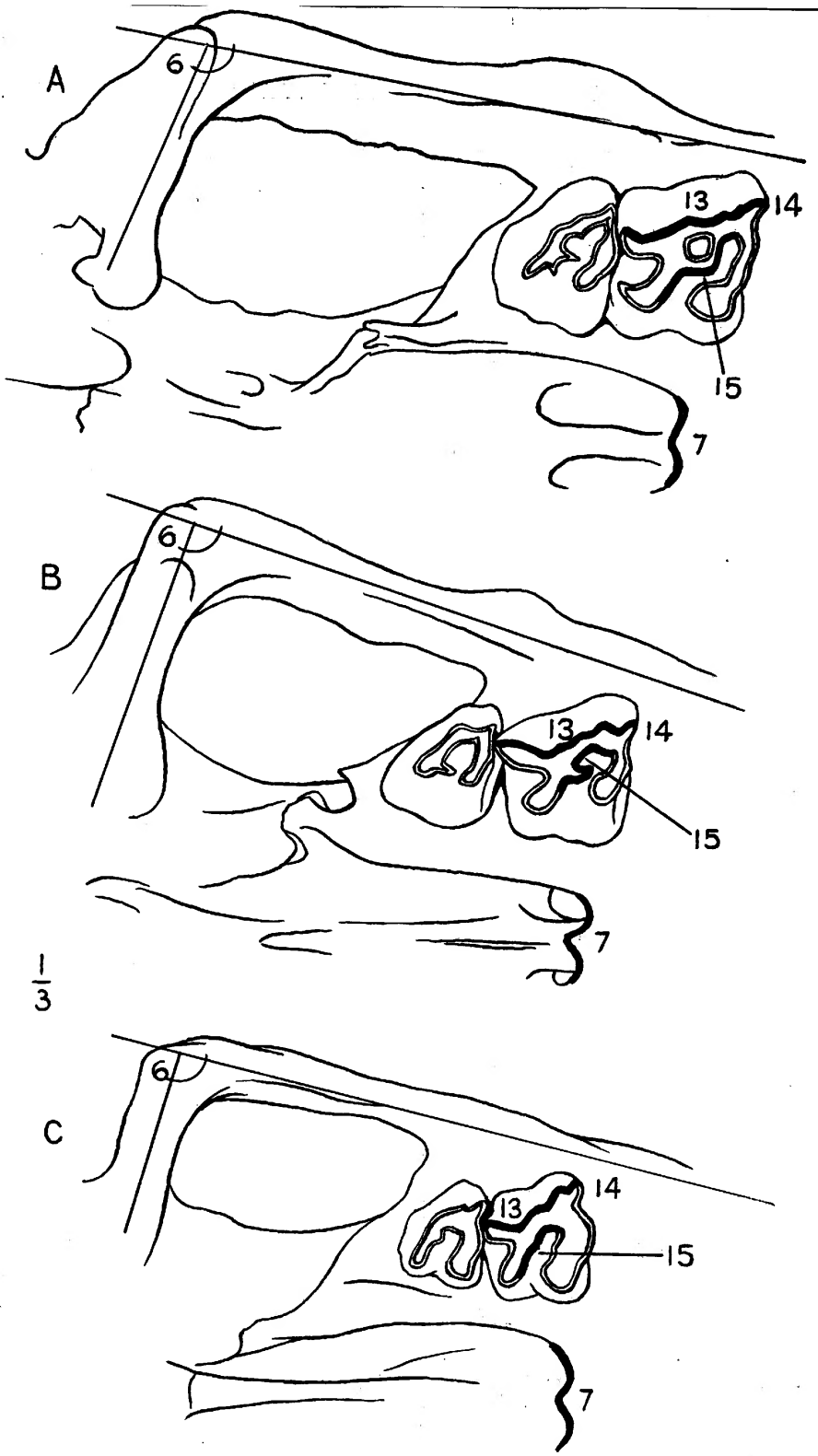


Fig. 2. Comparison of the glenoid and posterior palatal regions of the skull of (A) *Rhinoceros unicornis*, (B) *Rhinoceros sondaicus*, and (C) *Gaindatherium browni*. Palatal views of right side showing, from C to B to A: (6) increase in angle between glenoid and zygomatic arch, (7) decrease in median projection on posterior border of palate, (13) straightening of molar ectoloph, (14) reduction of parastyle buttress, (15) development of crochet and crista.

Compare the items with these same numbers on page 2.

Figures one-third natural size. A and B from Osborn, 1898; C from Colbert, 1934.

while the crochet and crista, although well developed (the latter often being reduplicated), do not join to enclose a medifossette as in *R. unicornis*. Thus it seems evident that *Rhinoceros sinensis* is a form of rather intermediate position between the two living species.

*Rhinoceros sivalensis*, on the other hand, would seem to be rather close to *Rhinoceros unicornis*. The extinct form is a large species, showing in the structure of the skull (the large horn boss, the deep saddle in the cranial profile, the forwardly inclined occiput, the depth of the skull and the like) a close approach to the modern Indian form. The cheek teeth in this

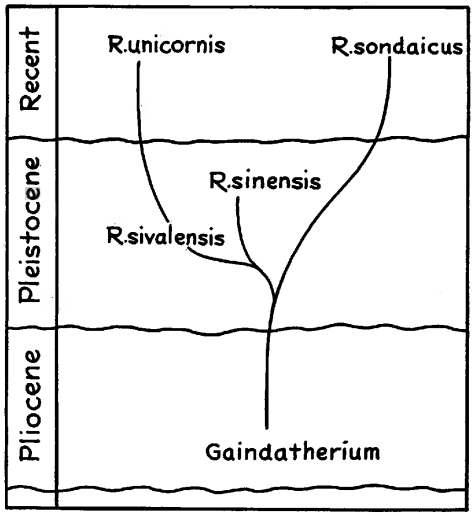


Fig. 3. Phylogenetic development of the genus *Rhinoceros*.

species are characterized by a rather flat ectoloph but by a certain retention of the parastyle buttress, while the crochet and crista have not reached that stage in development where they join to enclose a medifossette.

From these several comparisons certain facts emerge. *Rhinoceros sondaicus* may be distinguished from *Rhinoceros unicornis* by a large series of characters in the skull, the mandible and the dentition. In all of these characters the Javan rhinoceros is more primitive than the Indian form, so the development of the one from the other may be thought of as a "harmonic" growth affecting virtually all portions of the cranial and dental anatomy and proceeding in a single direction. Indeed, this development in the characters from *Rhinoceros sondaicus* to *Rhinoceros unicornis* is so marked that certain Pleistocene species of the genus occupy positions intermediate between the two modern forms, *Rhinoceros sinensis* being a truly intermediate type, *Rhinoceros sivalensis* being somewhat closer to the Indian species.

Consequently, it would appear that *Rhinoceros sondaicus*, though recent in age, is truly a persisting primitive form and anatomically may be regarded as at about a Lower Pleistocene or perhaps an Upper Pliocene stage of development. It approaches the Lower Pliocene genus *Gaindatherium*, being intermediate between this latter form and the more advanced Pleistocene and Recent species of *Rhinoceros* mentioned above. Therefore, *Rhinoceros sondaicus* upon the basis of present evidence is to be regarded as the most primitive member of the genus *Rhinoceros*, embodying in its structure the features which by further complications and developments became diagnostic for the Pleistocene species, *Rhinoceros sinensis* and *Rhinoceros sivalensis*, and for the Recent *Rhinoceros unicornis*. It is a true living fossil.

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